PHYLOGEOGRAPHIC STRUCTURE OF CO-DISTRIBUTED, UPLAND LINEAGES OF FROGS AND SNAKES ACROSS MOUNTAIN TOPS IN PENINSULAR MALAYSIA.

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By

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LIST OF ABBREVIATIONS

Abbreviation	Meaning
a.s.l.	above sea level
NADH	Nicotinamide adenine dinucleotide
PCR	Polymerase Chain Reaction
Cyt b	cytochrome b
ND1	NADH dehydrogenase subunit 1
IUCN	International Union for Conservation of Nature
LSUHC	La Sierra University Herpetological Collection
USMHC	Universiti Sains Malaysia Herpetological Collection
DOR	Dead On Road

STRUKTUR FILOGEOGRAFI KATAK DAN ULAR YANG MEMPUNYAI TABURAN BERTINDIH DAN BERKETURUNAN TANAH TINGGI YANG MERENTASI PUNCAK GUNUNG DI SEMENANJUNG MALAYSIA.

ABSTRAK

Kawasan pergunungan di serata dunia merupakan kawasan yang mempunyai kepelbagaian tinggi dan spesies-spesies endemik dan Semenanjung Malaysia tidak terkecuali. Struktur filogeografi tiga spesies katak gunung, *Metaphrynella pollicaris, Philautus petersi* dan *Philautus vermiculatus* dan tiga genus ular yang kebanyakannya dari kawasan pergunungan, *Macrocalamus, Calamaria* dan *Popeia* dibandingkan untuk mengenalpasti hubungan populasi allopatrik. Kerja lapangan dijalankan di beberapa lokasi tanah tinggi di seluruh semenanjung dan spesimen-spesimen dikumpul untuk perbandingan genetik. Tindakbalas rantaian polymerase (PCR) dijalankan untuk mengamplifikasi gen-gen mitokondria ND1 atau CytB, jujukan-jujukan gen disusun, dianalisis dengan analisis Bayesian dan Kebarangkalian Maksimum dan dimasukan dalam analysis integratif taxonomi bersama corak warna dan morphologi. Keputusan menunjukkan bahawa tiada satu corak menyeluruh dalam struktur filogeni takson-takson yang mempunyai taburan bertindih ini melintasi taburan mereka. Sebaliknya, analisis telah menunjukkan dua corak filogeografi yang bertentangan untuk katak dan ular. Populasi-populasi katak di atas gunung-gunung berbeza berhubungan rapat walaupun terasing dengan substruktur bersokongan lemah dalam corak filogeografi *Metaphrynella pollicaris* dan tiada substruktur langsung dalam dua spesies *Philautus*. Komposisi genetik yang agak serata ini menunjukkan bahawa spesies-spesies katak telah melalui proses perluasan taburan dalam sejarah mereka yang agak baru sahaja dan tidak mempunyai tempoh

masa panjang untuk populasi-populasi ini melalui proses perbezaan secara berasingan. Genus-genus ular pula menunjukkan struktur filogeografi yang jauh berbeza dengan corak substruktur yang mendadak dengan pencapahan yang sangat ketara di antara populasi-populasi allopatrik. Ini menunjukkan bahawa populasi-populasi ular mempunyai sejarah yang lebih lama berkemandiran secara berasingan dan seterusnya membentuk spesies-spesies berlainan. Satu spesies ular baru *Macrocalamus emas* sp. nov. dicirikan dan beberapa keturunan yang mempunyai genetik berbeza yang membuktikan terdapat beberapa spesies baru yang tersembunyi yang memerlukan penilaian teliti pada masa depan dikenalpasti dalam genera *Macrocalamus, Calamaria* dan *Popeia*. Walaupun taburan takson ini adalah akibat sejarah geografi Pentas Sunda yang dipengaruhi kitaran perubahan proses iklim glasiostatik, ekologi dan tabiat semulajadi yang berbeza di antara spesies-spesies berlainan telah mempengaruhi tindak balas mereka terhadap perubahan itu dan taburan mereka kini adalah bayangan interaksi tersebut. Secara keseluruhan, kepelbagaian dalam genus ular amat terkurang anggar dan terdapat banyak spesies-spesies kriptik lagi yang masih belum dicirikan secara rasmi dengan perbandingan yang lebih teliti. Penemuan ini mempunyai implikasi terhadap pemuliharaan spesies-spesies endemik yang bertaburan sempit di kawasan pergunungan kerana ancaman perubahan iklim mampu melenyapkan spesies-spesies ini sebelum mereka dan dicirikan secara rasmi.

PHYLOGEOGRAPHIC STRUCTURE OF CO-DISTRIBUTED, UPLAND LINEAGES OF FROGS AND SNAKES ACROSS MOUNTAIN TOPS IN PENINSULAR MALAYSIA.

ABSTRACT

Montane regions around the world are areas of high diversity and endemism and Peninsular Malaysia is no different. The phylogeographic structure of three species of montane frogs, *Metaphrynella pollicaris*, *Philautus petersi* and *Philautus vermiculatus* and three genera of largely montane snakes, *Macrocalamus*, *Calamaria* and *Popeia* were compared to ascertain the relationships of the different allopatric populations. Field work was conducted at various montane sites across the country and specimens were collected for genetic comparison. Following PCR amplification for the ND1 or CytB mitochondrial genes, sequences were aligned, analysed using Bayesian and Maximum likelihood analyses and included in an integrative taxonomic analysis using colour pattern and morphology. The results reveal no single overarching pattern in the phylogenies of these co-distributed species across their range. Instead, the analyses reveal two very opposing phylogeographic patterns in the frogs and the snakes. The populations of frogs on separated mountain tops are very closely related to each other with only weakly supported substructuring observed in amongst the *Metaphrynella pollicaris* populations and no substructuring observed among the two species of *Philautus*. This fairly homogeneous genetic makeup observed, despite their geographic isolation, indicates a rapid range expansion in the recent past and that these populations have not had sufficient time to diverge in isolation. In contrast, the snakes revealed marked levels substructuring in their molecular phylogenies with deep divergences amongst allopatric populations. This indicates a much longer history of separation in these groups which have given

the populations ample time to evolve along their own individual trajectories leading to their genetic differentiation and subsequent speciation. A new species of reed snake *Macrocalamus emas* sp. nov is described and a number of genetically distinct lineages that correspond to cryptic candidate species in need of future taxonomic reappraisal were uncovered within the genera *Macrocalamus*, *Calamaria* and *Popeia*. Although the distributions of the various taxa have been influenced by continuous changes from glacioeustatic driven climatic processes that affected the geography of Sundaland, the different ecologies and natural histories of these lineages have affected how they have responded and lead to their present day distributions. Overall, diversity in the snake genera has been underestimated and many cryptic lineages abound that are putative species awaiting formal recognition by more thorough comparisons. These discoveries have implications for the conservation of these narrow range upland endemics as the threat of global warming threatens to eliminate some of these undescribed species even before they are given formal taxonomic recognition.

CHAPTER 1. INTRODUCTION

1.1 Brief overview of the study

It has been said all too often that Malaysia is a treasure trove of biological diversity and one of the few countries that can boast as a megadiverse hotspot (Sodhi *et al*. 2004; Grismer, 2011a; Das & van Dijk 2013). Malaysia is divided into two parts, East Malaysia that covers the top quarter of the island of Borneo and is composed of the states of Sabah and Sarawak and West Malaysia (referred to as Peninsular Malaysia henceforth) that is a peninsula that stretches south from Indochina and forms the very tip of continental Asia.

Strategically located between Indochina to the north and Indo-Australian archipelago to the south, Peninsular Malaysia stretches like a long biological corridor for the exchange of plants and animals between the two regions and is the focus of this study. Countless numbers of species of which many yet remain undescribed are found from the high mountains to lush lowland rainforest, swamps, coastlines and in the rich shallow seas surrounding the many thousands of islands surrounding Sundaland (Bickford *et al*. 2007; Sodhi *et al*. 2004, 2010).

Ever since Darwin first sailed to the Galapogos Islands, people have always thought of islands as a paradise that drives the evolution of a menagerie of different species. Pioneering work by L.L. Grismer and his team in the 1990's discovered many new species of reptiles and amphibians in the Seribuat Archipelago (Grismer 2011b; Grismer *et al*. 2002, 2004a, 2006b). Similar surveys on other island archipelagos around Peninsular Malaysia such as the Langkawi, Redang and Perhentian groups of islands had similar results (Grismer *et al*. 2006c, 2011a). However mainland Peninsular Malaysia supports other habitats still in need of

attention such as the vast innumerable number of limestone karst outcrops, hills and mountain peaks. These habitats have already shown to harbour many species new to science (Chan *et al*. 2014a; David & Pauwels 2004; Grismer *et al*. 2012a, 2013a,b, 2014a,b, 2015a,b; Grismer & Quah 2015; Loredo *et al*. 2013; Matsui *et al*. 2009, 2014; Vogel & David 1999; Vogel *et al*. 2004; Wood *et al*. 2008, 2009; Zug 2010) and continued work will surely reveal many more in the years to come.

Mountain tops are also effectively islands in their own right and are 'sky islands' that are separated from each other by vast intervening lowland 'seas'. This isolation has driven the evolution of many unique and peculiar forms (Heald 1951; McCormack *et al*. 2009). Early colonial settlers in Peninsular Malaysia took advantage of the cool conditions in the highlands and used them as retreats and opened them up to agriculture, producing crops such as tea and strawberries. As a result, dozens of new species were discovered and described from many early hill stations in Peninsular Malaysia such as Maxwell's Hill, Cameron Highlands and Frasers Hill (Boulenger 1886a,b, 1889b, 1900a,c,d, 1912; Smedley 1931a; Nicholls 1949; Laidlaw 1901; Smith 1924; Werner 1900). In recent years, expeditions into previously unexplored mountainous regions have discovered many new species of amphibians and reptiles (Chan *et al*. 2014a; Grismer *et al*. 2013a, 2014a,b, 2015b,c; Sumarli *et al*. 2015). Even in previously sampled locations, renewed interest in the herpetofauna there has resulted in a plethora of new discoveries (David & Pauwels 2004; Grismer *et al*. 2011b, 2015a; Grismer & Quah 2015; Vogel & David 1999; Vogel *et al*. 2004; Wood *et al*. 2008, 2009).

Some of these recently described species have been completely novel such as Tung's narrow-mouthed frog (*Gastrophrynoides immaculatus*), Penang Limbless Skink (*Larutia penangensis*) and Gunung Tebu Bent-toed Gecko (*Cyrtodactylus*

tebuensis) (Chan *et al*. 2009; Grismer *et al*. 2011b, 2013a) while the others are the result of closer examination of what was once thought to be a previously nominal, widespread species such as the Northern Creek Frog (*Limnonectes utara*), Southern Creek Frog (*L. selatan*), Bintang Range Mountain Horned Lizard (*Acanthosaura bintangensis*), Titiwangsa Range Mountain Horned Lizarrd (*A. titwangsaensis*), members of the Banded Geckos (*Cyrtodactylus pulchellus*) complex, Temiah Rock Gecko (*Cnemaspis temiah*), Titiwangsa Slender Gecko (*Hemiphyllodactylus titiwangsaensis*), Mirkwood Forest Slug Snake (*Asthenodipsas lasgalenensis*), Chanard's Reed Snake (*Macrocalamus chanardi*), Schulz's Reed Snake (*M. schulzi*), Vogel's Reed Snake (*M. vogeli*), Siamese Peninsula Pitviper (*Popeia fucata*) and Cameron Highlands Pitviper (*P. nebularis*) (David & Pauwels 2004; Grismer *et al*. 2012a, 2014b; Loredo *et al*. 2013; Matsui *et al*. 2014; Vogel *et al*. 2004; Vogel & David 1999; Wood *et al*. 2009; Zug 2010). Many of these discoveries have been made using modern techniques in integrative taxonomy, the addition of molecular data to compliment classical taxonomy using morphology. These are referred to as cryptic species. Different populations at different locations might look superficially similar but they are genetically different and sometimes do not share a similar evolutionary history (Grismer *et al*. 2012a, 2013b; Loredo *et al*. 2013; Matsui *et al*. 2014).

After nearly two decades of work on the lizard fauna of Peninsular Malaysia, L.L. Grismer discovered more than three dozen species new to science and many more species await formal description (Grismer 2011a). This intense scrutiny of the lizard fauna of Peninsular Malaysia over the last two decades has now culminated in the identification of many of the cryptic species that have been subsequently formally described (Grismer *et al*. 2012a,b, 2013a,b, 2014a,b, 2015a,b,c; Johnson *et*

al. 2012). These works have only been possible through the dedicated efforts of field biologist to collect specimens from various locations, and amass tissue samples needed for these large scale comparisons. This has enabled the phylogenetic examination of some genera in detail such as the Rock geckos (*Cnemaspis*), Banded geckos (*Cyrtodactylus pulchellus*) and Marbled Bent-toed Geckos (*C. quadrivirgatus*) groups, Slender geckos (*Hemiphyllodactylus*), Larut Skinks (*Larutia*) and Green-Crested Lizards (*Bronchocela*) (Grismer *et al*. 2011b, 2012a, 2013b, 2014a, 2015a,b; Johnson *et al*. 2012). Some other groups are in the works such as the little skinks of the genus *Tyttoscincus,* different populations of the Blotched Forest Skink (*Sphenomorphus praesignis*) and the Horned Tree Lizards (*Acanthosaura*). (in prep and in press).

These works have in turn laid the foundation for the comparison for some of the other herpetofaunal groups, namely the frogs and snakes of Peninsular Malaysia. Recently, a few species of montane snakes and frogs were described through integrative taxonomy as well such as new species of slender toad (*Ansonia*) and Slug Snake (*Asthenodipsas*) (Chan *et al*. 2014a; Loredo *et al*. 2013). Similar to the many number of cryptic lizard species, there are a number of frog and snake species that are widespread and have distributions on the many mountain ranges ranging across the country (Lim & Leong 2003b; Lim *et al*. 2002; Grismer *et al*. 2010a; David & Pauwels 2004; Vogel *et al*. 2004; Vogel & David 1999). Each one of these different species has different ecologies and life histories.

Among the different snake genera chosen for comparison in the study, each group differs in their natural history. Reed snakes of the genus *Calamaria* and *Macrocalamus* are terrestrial, semi-fossorial snakes that burrow under leaf litter, debris and loose soil (Baker & Lim 2008; Inger & Marx 1965; David & Pauwels

2004; Vogel & David 1999). They differ again from each other in that members of the genus *Calamaria* are nocturnal (Inger & Marx 1965; Grismer 2011b) while species in the genus *Macrocalamus* have members that are diurnal, crepuscular or nocturnal (Lim 1963a; Norsham & Lim 2002; David & Pauwels 2004; Vogel & David 1999; personal obervations). Both these groups feed largely on soft-bodied invertebrate prey such as earthworms (Baker 2014; Tan & Yeo 2013) while some literature reports that the larger *Calamaria* and *Macrocalamus* species such as the Variable Reed Snake (*C. lumbricoidea*) and Tweedie's Reed Snake (*M. tweediei*) are known to feed on small skinks and geckos (Lim 1956; 1963a; Cox *et al*. 1998). In contrast, vipers of the genus *Popeia* are arboreal snakes that are found in trees and vegetation. They are also nocturnal, have prehensile tails and coil up on amongst the branches to ambush prey (Grismer 2011b; Grismer *et al*. 2006a; Sumontha *et al*. 2011). These snakes are known to take frogs and lizards as part of their diet (personal observation).

All the frogs are arboreal but they differ in their reproductive biology. The two species of bush frogs, Peter's Bush Frog (*Philautus petersi*) and the Vermiculated Bush Frog (*P. vermiculatus*) undergo direct development. The eggs are laid in moist, sheltered areas and hatch into froglets (Grismer 2011b; Inger & Voris 2001; Malkmus *et al*. 2002; Marmayou *et al*. 2000). The Malaysian tree-hole frog (*Metaphrynella pollicaris*) as its common name suggest is a phytolem breeder. Males call from tree holes to attract mates and when successful the female deposits her eggs inside the water-filled tree hole (Malkmus *et al*. 2002).

The different taxa display different phylogeographic structures. The frogs showed very weakly supported phylogeographic sub-structuring which is indicative of a single, recently expanded, widespread population. This similar topology is seen

in *Cyrtodactylus quadrivirgatus* that was examined by Johnson *et al*. (2012) who noted that despite having distinct populations with variable colour patterns associated with certain localities and habitats, they were genetically very similar with evidence of interpopulational gene flow. The topology of *Philautus* and *Metaphrynella* differ from that of *Ansonia* which shows distinct structuring with specific species being endemic to certain localities (Chan *et al*. 2014a). The frogs *P. petersi*, *P. vermiculatus* and *M. pollicaris* that are found throughout the Bintang, Titiwangsa and Timur ranges in Peninsular Malaysia and show great uniformity in their genetic makeup (Grismer *et al*. 2010a; Leong & Lim 2003b; Lim *et al*. 2002). In contrast on each of these mountain ranges there is an endemic species of *Ansonia*. In the Bintang range it is Malayan Slender Toad (*A. malayana*), in the Titiwangsa Range it is Jeetsukumaran's Slender Toad (*A. jeetsukumarani*) while in the Timur Range the recently described Mossy Slender Toad (*A. lumut*) (Chan *et al*. 2014a).

The snakes on the other hand have very deep branches in their trees indicating a much older phylogenetic history. This was a more commonly observed in the populations of mountain top lineages (Grismer *et al*. 2011b, 2012a, 2013b, 2014a,b). For example, in the genus *Macrocalamus*, most members of this genus are endemic to specific mountain tops (Lim 1963a; Norsham & Lim 2002; David & Pauwels 2004; Vogel & David 1999). *Macrocalamus chanardi* which is currently considerd to be a wide ranging species found in the Bintang and Titiwangsa ranges is shown here to be very distinct genetically with respect to their separate upland populations. The other wide ranging species, the Lateral-blotched Reed Snake (*M. lateralis*) may also prove to be similar with the acquisition of additional genetic material. The steep slopes of these mountains coupled with the specific microhabitat and niche requirements of these species create physical and ecological barriers to

their dispersal. To this the added selection pressures of the long geological history of these mountains with the cyclical, fluctuating changes of sea levels has led to the fragmentation of populations and species divergence (Sathiamurthy & Voris 2006; Voris 2000; Woodruff 2010; Woodruff & Turner 2009).

These discoveries underline the importance of continued herpetological surveys into other unexplored mountainous regions with proper inventory and record keeping. Only when we are equipped with a sound understanding of the biological diversity that is harboured in our mountains can we effectively safeguard them. Most of the world's biodiversity is concentrated along mountain ranges (Grenyer *et al*. 2006) and Peninsular Malaysia is no different. It has already been shown that a significant number of Peninsular Malaysia's herpetofauna are small, cryptic montane species that despite having no commercial value are probably some of the species most at risk of extinction given the continuing trends in development in Malaysia (Grismer 2011a; Grismer *et al*. 2011b, 2013b, 2014b). Montane ecosystems are some of the most threatened on the planet (La Sorte & Jetz 2010) and biodiversity is increasingly threatened by the hand of man and development.

Despite the great advances we have made in unravelling the evolutionary relationship of many groups of amphibians and reptiles that led to the discovery of many new species, the history of many other groups is still largely unknown. Some of these groups are extremely rare and poorly represented in collections and some are only known from a handful of type specimens such as Jason's Reed Snake (*Macrocalamus jasoni*) (Grandison 1972; Vogel & David 1999). Due to this paucity of material and lack of tissue for molecular analyses, only hypothesized relationships can be inferred on the phylogenetic placement of these species. More intensive exploration and collection to locate these missing species will overcome this small

artefact of the lack of genetic material and shed light on their past hidden deep within their genes.

1.2 The Rationale and Importance of this study

To understand the historical context and reasons behind the high levels of diversity and endemism in upland communitites we need to look into the phylogenetic relationships of their different taxa. These relationships will reveal the driving forces behind their levels of speciation or specialisation and provide us with clues as to the trajectory of their evolutionary future. This is especially true in Peninsular Malaysia where the unique, phylogeographic patterns of many upland endemics are a consequence of their unique and varied evolutionary histories coupled with their unique and varied life histories (Grismer *et al.* in prep.). Understanding this inextricable relationship will provide insight as to how climate change may affect the trajectory of phylogeographic change and we can begin to entertain conservation measures to mitigate potential threats in the face of global warming.

1.3 Hypotheses of the study

Firstly we know that there has been only one environmental history (tectonic and climatic) for Peninsular Malaysia and so all lineages of this study have been subjected to this history. Therefore if we see that:

1. Different species of upland frogs and snakes found at the same locations across the same upland landscape show similar patterns of phylogenetic sub-structuring then they have responded similarly to past geological and climatic events.

2. If there is no overarching phylogenetic pattern among the different species across the same montane locations then their current distribution may be a reflection of

differences in life histories that affected their dispersal capabilities during glacial maxima when these upland populations would have been able to exchange genes.

1.4 Objectives of the study

1. To examine the phylogenetic relationship of two genera of frogs composing of three species and three genera of snakes composing of 14 species that are co-distributed across mountain tops in Peninsular Malaysia.

2. To compare the phylogeographic structure amongst the different species across a common landscape and how it relates to the past geological history and the current life histories of the species.

3. To compare the phylogeographies of the study taxa to the phylogeographies of the many species of lizards that have previously been examined by Grismer *et al*. 2011b, 2012a, 2013b, 2014a,b, 2015a,b and Johnson *et al*. 2012.

4. To flag candidate species in need of future taxonomic reappraisal.

CHAPTER 2. LITERATURE REVEW

2.1 History of montane herpetology in Peninsular Malaysia

Tropical montane ecosystems are regions of high diversity and endemism. This phenomena is not just restricted to Sundaland, Indochina and the Indo-Australian archipelago but is evident in all upland tropical regions (Grenyer *et al*. 2006). A rich diversity of reptile and amphibian species, many of them endemics are found in tropical mountane ecosystems around the world such as the neotropics (Crawford *et al*. 2010; Heinicke *et al*. 2009; Hofer & Bersier 2001; McCranie & Castaňeda, 2005; McCranie *et al*. 2005; Myers *et al*. 2007; Rivas *et al*. 2005; Rovito *et al*. 2012; Streicher *et al*. 2009; Townsend *et al*. 2010; Vaira 2002; Wake 1987; Wilson & McCranie 2004a,b), east Africa (Blackburn 2008; Burgess *et al*. 2007; Gonwouo *et al*., 2006, 2007; Loader *et al*. 2011; Malonza *et al*. 2010; Menegon *et al*. 2004, 2008, 2011; Stipala *et al*. 2011; Zimkus & Gvoždĩk 2013), Madagascar (Andreone *et al*. 2007; Glaw *et al*. 2011; Randrianantoandro et al., 2009; Rakotoarison *et al*. 2012; Raxworthy & Nussbaum 1996; Vences *et al*. 2002) , Australia & New Guinea (Allison *et al*. 1996; Austin *et al*. 2010; Chapple *et al*. 2005; Schleip 2008; Kraus & Allison 2009) and the mountainous belt of the Western Ghats and Sri Lanka (Abraham *et al*. 2013; Aravind *et al*. 2007; Bauer *et al*. 2007; Bhupathy *et al*. 2012; Biju 2001; Biju & Bossuyt, 2009; Biju *et al*. 2009, 2010, 2011, 2014a,b; Gunatileke *et al*. 2008; Jobin & Nameer 2012; Karunarathna *et al*. 2008; Mirza *et al*. 2014; Molur 2008; Nair *et al*. 2012; Padhye *et al*. 2013; Pyron *et al*. 2013; Seshadri *et al*. 2012; Zachariah *et al*. 2011).

The uplands of Peninsular Malaysia are part of this cosmopolitan complex of ecosystems and have a rich history of past research. Many noted herpetological

collections were made in the mountainous regions of the country at the turn of the 19th century. The highlands of Peninsular Malaysia are characterized by three main mountain systems, the Bintang Range in the northwestern corner of Peninsular Malaysia, the Titiwangsa range that stretches along the countries central spine and the Timur Range that is composed on a collection of peaks in the east (Fig. 2.1) (Grismer 2011a). The first of these, the Bintang Range is a comparatively short range of approximately 140 km that stretches from the central portion of the state of Perak and crosses into the eastern corner of Kedah and onward into the Thai border and terminates near Jalor in Yala Province, Thailand (Grismer *et al*. 2010a). The Titiwangsa Range runs nearly the entire length of the country has its origins well north of the Malaysian-Thai border and extends southwards for nearly 500 km. Some of the tallest mountains are found along its' length such as Gunung Korbu (2183 m), Gunung Irau (2110 m) as well as the famous Gunung Brinchang (2031 m). Much of this massif does not dip below 1000 m in elevation and it divides the country into eastern and western halves. The last of the major mountain systems is the Timur Range in the far east of the country. Unlike the two preceding mountain ranges that are a clear, distinct, elevated belt of ridges and peaks, the Timur Range is a complex array of semi-isolated peaks, plateaus and ranges in the states of Kelantan, Terengganu and Northern Pahang (Grismer 2011a). Here too is where the tallest peak in Peninsular Malaysia is located, Gunung Tahan that towers at 2187m a.s.l. in elevation and is the type locality of four montane reptiles endemic to Peninsular Malaysia; Robinson's Anglehead Lizard (*Malayodracon robinsoni* (Boulenger 1908)), Dring's False Garden Lizard (*Pseudocalotes dringi* Hallermann & Böhme 2000), Tahan Mountain Forest Skink (*Sphenomorphus cophias* Boulenger 1908) and Vogel's Reed Snake (*Macrocalamus vogeli* David & Pauwels, 2004).

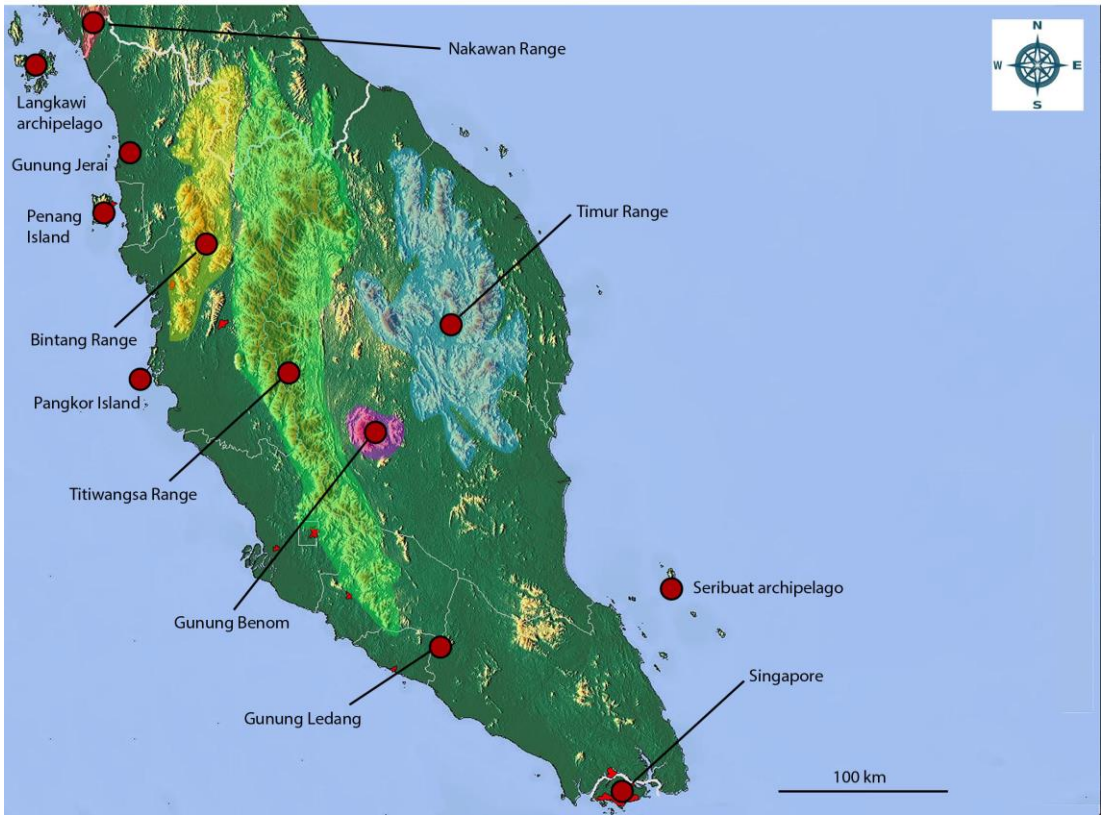

Figure 2.1. Map of the main mountain ranges in Peninsular Malaysia and other prominent localities.

The early British settlers in the country built many retreats in the highlands that opened up mountainous regions to early exploration and in turn enabled many new species to be collected and subsequently described at the turn of the last century (see Leong & Lim 2003b; Lim *et al*. 2002; Grismer 2011a; Das & Norsham 2007). At the forefront of these many locations is Maxwell Hill or as it is now more commonly known as Bukit Larut in Taiping, Perak as it is the type locality for the most number of species in Peninsular Malaysia (Grismer *et al*. 2010a, 2013b, 2015a). Taking into account the all the various locations along this mountain range where type material has originated such as Gunung Hijau, Gunung Inas and Bukit Larut, more species of amphibians and reptiles have been discovered and described from the Bintang Range than anywhere else in Peninsular Malaysia, 27 species in total

(Grismer *et al*. 2010a, 2013b, 2015a). A total of nine amphibian species, thirteen lizards and five snakes have been described from these mountains. One of the early naturalists to report on the herpetofauna from here was Flower (1896) and many of the species he collected were passed to George Albert Boulenger to describe. In total Boulenger described 15 species from the Larut Hills, all of which are still valid until today. The species which he described are; Variable Slender Litter Frog (*Leptolalax heteropus* Boulenger 1900a); Long-legged spadefoot toad (*Xenophrys longipes* (Boulenger 1886a)); Larut Hills Chorus Frog (*Microhyla annectens* Boulenger 1900a); Butler's Chorus Frog (*M. butleri* Boulenger 1900a); Larut Torrent Frog (*Amolops larutensis* (Boulenger 1899b)); *Philautus vermiculatus* (Boulenger 1900a); Pied Wart Frog (*Theloderma asperum* (Boulenger 1886b)); Dusky Gliding Lizard (*Draco formosus* Boulenger 1900a); Larut Slender Gecko (*Hemiphyllodactylus larutensis* (Boulenger 1900a)); Larut Hills Larut Skink (*Larutia larutensis* (Boulenger 1900c)); Butler's Forest Skink (*Sphenomorphus butleri* (Boulenger 1912)); Starry Forest Skink (*S. stellatus* (Boulenger 1900a)); *S. praesignis* (Boulenger 1900a); Mountain Slug Snake (*Asthenodipsas vertebralis* (Boulenger 1900c)) and Butler's Wolf Snake (*Lycodon butleri* Boulenger 1900d) (Grismer *et al*. 2010a, 2013b).

Since then many other noted herpetologist have worked in this area and described a number of additional species, such as Robert F. Inger who described *Ansonia malayana* from Bukit Larut in 1960. Edward H. Taylor described the Larut Caecilian (*Caudacaecilia larutensis*) in 1960, while L.L Grismer and his colleagues have described *Acanthosaura bintangensis* Wood, Grismer, Grismer, Norhayati, Chan & Bauer, 2009; McGuire's Rock Gecko (*Cnemaspis mcguirei* Grismer, Grismer, Wood & Chan, 2008); False McGuire's Rock Gecko (*Cnemaspis*

pseudomcguirei Grismer, Norhayati, Chan, Belabut, Muin, Wood & Grismer, 2009); Bintang Range Upland Banded Gecko (*Cyrtodactylus bintangtinggi* Grismer, Wood, Quah, Shahrul, Muin, Sumontha, Norhayati, Bauer, Wangkulangkul, Grismer & Pauwels, 2012a) and *Asthenodipsas lasgalenensis* Loredo, Wood, Quah, Shahrul, Greer & Grismer, 2013. Other species that have been described from here are the Larut False Garden Lizard (*Pseudocalotes larutensis* Hallermann & McGuire, 2001) from Bukit Larut, the Hartert's Slender Gecko (*Hemiphyllodactylus harterti* (Werner 1900)) from Gunung Hijau, the Gunung Inas Keelback (*Hebius inas* (Laidlaw 1901)) from Gunung Inas and *Macrocalamus chanardi* David & Pauwels, 2004 from Bukit Larut. The latest addition to the growing list of herpetofauna that have Bukit Larut designated as their type locality is the Shen Long Green-Crested Lizard (*Bronchocela shenlong* Grismer, Wood, Lee, Quah, Shahrul, Ngadi & Sites 2015a).

Cameron Highlands is another well-known montane site in Peninsular Malaysia with a rich herpetological history. A number of early naturalist collected at Cameron Highlands such as G.H. Sworder in 1927, K.B. Williamson between 1930-1932, R. Hanitsch in 1930, H.R. Henderson in 1930, C.P. Navaratnam in 1932, G.P. Wilkins in 1933, M.W.F. Tweedie in 1938, G.H. Lowe in 1940, R. Lever in 1947, J.A. Reid in 1952, B.L. Lim in 1959 and C.C. Chua in 1967 (Lim *et al*. 2002). Cecil Boden-Kloss who was the Director of the Raffles Museum between 1923 and 1932 and Frederick Nutter Chasen, Curator of the Raffles Museum at that time conducted a joint expedition with the Federated Malay States Museum to Cameron Highlands and Gunung Angsi in Negeri Sembilan (Das & Norsham 2007). However it was Smedley who was the first to produce a comprehensive report on the herpetofauna found there in 1931 and he went on to describe one new species of frog, the Tanah Rata Frog (*Limnonectes nitidus*) and two new species of snakes, the Red Mountain

Keelback (*Hebius sanguineum*) and Williamson's Reed Snake (*Collorhabdium williamsoni*) in that paper (Smedley 1931a). The latter was named in honour of its collector K.B. Williamson that had collected the type series at Tanah Rata, Cameron Highlands. Along the way a number of other species and subspecies were discovered and subsequently described from the area such as the Yellow-throated False Garden Lizard (*Pseudocalotes flavigula* (Smith 1924)), Cameron Highlands Forest Skink (*Sphenomorphus cameronicus* Smith 1924), Three-banded Larut Skink (*Larutia trifasciata* (Tweedie 1940)), Red Mountain Rat Snake (*Oreocryptophis porphyracues laticinctus* (Schulz & Helfenberger, 1998)), *Macrocalamus tweediei* Lim 1963a, *Macrocalamus schulzi* Vogel & David 1999, *Popeia nebularis* (Vogel, David & Pauwels 2004), Banjaran Frog (*Pulchrana banjarana* (Leong & Lim 2003a)), Yong's Narrow-Mouth Frog (*Kalophrynus yongi* Matsui 2009), Small Litter Frog (*Leptolalax kecil* Matsui, Belabut, Norhayati & Yong 2009), *Hemiphyllodactylus titiwangsaensis* Zug 2010, *Cnemaspis temiah* Grismer, Wood, Anuar, Riyanto, Ahmad, Muin, Sumontha, Grismer, Chan, Quah & Pauwels 2014 and the Titiwangsa Forest Skink (*Sphenomorphus senja* Grismer & Quah 2015). Recent field work in the region have discovered other species awaiting description such as a new species of False Garden Lizard (*Pseudocalotes* (Grismer *et al*. in prep.)), Little Brown Forest Skink (*Tyttoscincus* (Grismer *et al*. in prep)) and a new Reed Snake (*Macrocalamus* (described in this dissertation)).

Further south along the Titiwangsa Range sits Fraser's Hill, which is a famed montane birding location in Peninsular Malaysia (Strange 2004), has also been a location of herpetofaunal surveys. Smith (1922) was the first to report on some of the amphibians and reptiles found there and there were only sporadic reports of the herpetofauna before Leong & Lim (2003b) consolidated it into a checklist. This was

followed up by an updated checklist by Norhayati *et al*. (2011) that had a host of errors such as the listing of the Web-footed Bent-toed Gecko (*Cyrtodactylus brevipalmatus*) instead of the Beautiful Bent-toed Gecko (*Cyrtodactylus elok*), *Hemiphyllodactylus harterti* instead of *Hemiphyllodactylus* cf. *titiwangsaensis* and *Macrocalamus lateralis* instead of *Macrocalamus chanardi* (see David & Pauwels 2004; Grismer 2008b, 2011a; Grismer *et al*. 2013b, 2015b). A number of early collectors surveyed the area such as R. Hanitsch in 1907, C.S. Navaratnam in 1928, E.O. Shebbeare in 1928 and 1947, G.H. Sworder in 1933 and N.T. Cho in the 1950's (Leong & Lim 2003b). Historically this mountain served as the type locality for the Fraser's Hill Rock Gecko (*Cnemaspis flavolineata* (Nicholls 1949)) and Titiwangsa Larut Skink (*Larutia miodactyla* (Boulenger, 1903)) but there have been other recent discoveries here such as *Ansonia jeetsukumarani*, Wood, Grismer, Norhayati & Juliana, 2008, *Acanthosaura titiwangsaensis*, Wood, Grismer, Grismer, Norhayati, Chan, Bauer, 2009, Fraser's Hill Forest Skink (*Sphenomorphus bukitensis* Grismer, 2007) and the Southern Titiwangsa Banded Gecko (*Cyrtodactylus australotitiwangsaensis* Grismer, Wood, Quah, Shahrul, Muin, Sumontha, Norhayati, Bauer, Wangkulangkul, Grismer & Pauwels, 2012a).

In the far east, Dring (1979) published on the amphibians and reptiles of Gunung Lawit, a mountain that has not been explored since his descriptions of the lizards Lawit Mountain Rock Gecko (*Cnemaspis argus*) and *Cyrtodactylus elok*. Only recently have expeditions been mounted to a its neighbouring peak Gunung Tebu which have resulted in the rediscovery of *C. argus* along with more species new to science such as *Ansonia lumut, Cyrtodactylus tebuensis,* Timur Range Banded Gecko (*C. timur*), Tebu Mountain Slender Gecko (*Hemiphyllodactylus tehtarik*) and the Spotted Slender Gecko (*H. bintik*) (Chan *et al*. 2014a; Grismer *et al*.

2013a,b, 2014a, 2015b). A full report of the amphibians and reptiles found there has recently been published (Sumarli *et al*. 2015). Another mountain in the Timur range that has only recently been surveyed is Gunung Stong in Kelantan that has also resulted in the discovery of two species new to science, the Stong Mountain Rock Gecko (*Cnemaspis stongensis*) and the Jelawang Banded Gecko (*Cyrtodactylus jelawangensis*) (Grismer *et al*. 2014a, b). To the south east of the Titiwangsa Range lies the isolated massif Gunung Benom which was surveyed in the 1967 by Grandison and published later on (Grandison 1972). This survey made many notable findings, especially a number of rare snakes such as the Royal Tree Snake (*Gonyosoma margaritatum*), Sarawak Mountain Keelback (*Hebius sarawacense*) and the first record of the Slender Wolf Snake (*Lycodon albofuscus*) for Peninsular Malaysia. This expedition also resulted in the discovery of a new species of *Macarocalamus, M. jasoni* that is known only from the peak of Gunung Benom and a new frog, the Sungai Lembing Slender Toad (*Ansonia latirostra*) (Grismer 2006a). No subsequent expeditions have revisited this peak since the trails seem to have been overgrown.

There are other lesser ranges in the country like the Nakhawan range in the very far north of the country at the border with Thailand and other scattered and isolated mountains around the country such as Gunung Jerai, Gunung Belumut, Gunung Panti and Gunung Ledang (Grismer 2011a). Some of these isolated mountains such as Gunung Jerai and Gunung Ledang have been surveyed in the past while others remain unexplored. Gunung Ledang in Johor represents the isolated southern extent of the central Titiwangsa Range. This mountain reaches 1276m a.s.l. in elevation was historically known as Mount Ophir and even hosted the famous naturalist Alfred Russel Wallace who spent a short time collecting here in 1854

(Wallace 1869). Despite this, there has only been passing mention of the herpetofauna of the area such as scattered records of a few snakes and a number of lizards in Batchelor (1954, 1958), Tweedie (1957, 1983) and Grismer (2011a). Quah *et al*. (2014) recently published a preliminary checklist of the herpetofauna found at Gunung Ledang and serves as the type locality of the recently described Peninsular Rock Gecko (*Cnemaspis peninsularis* Grismer, Wood, Shahrul, Riyanto, Ahmad, Muin, Sumontha, Grismer, Chan, Quah & Pauwels 2014). Similar to Gunung Ledang, Gunung Jerai is another isolated coastal massif reaching 1200m a.s.l. located near the town of Gurun in Kedah, northwestern Peninsular Malaysia (WWF Malaysia 1977). This mountain is the type locality of the Mount Jerai Frog (*Odorrana monjerai* Matsui & Jaafar 2006) and the Tiger Rock Gecko (*Cnemaspis harimau* Chan, Grismer, Shahrul, Quah, Muin, Savage, Grismer, Norhayati, Remigion & Greer 2010a). Prior to this the herpetofauna of the mountain had been reported by Robinson and Kloss (1916), Sukumaran (2005) and Shahrul *et al*. (2006). Gunung Jerai is an isolated mountain that has never been joined to any other mountain system and even existed as an island numerous times in the past when changing sea levels inundated the surrounding lowlands. Today Gunung Jerai is surrounded by a vast expanse of plains that do not exceed 15 m a.s.l. in elevation and is separated from the Indian Ocean on its west and from the next closest peak Penang Hill on Penang Island approximately 35 km to the southwest (Bradford 1972; WWF Malaysia 1977).

Many island archipelagos around the nation are composed of notable peaks as well such as Gunung Machinchang and Gunung Raya on Langkawi Island, Penang Hill on Penang Island and Gunung Kajang of Tioman Island (Grismer 2011b; Grismer *et al*. 2002, 2004a, 2006b). Penang Island is comparable to the Bintang

Range as it has been a place of great herpetological significance due to the islands long history during the colonial era (Grismer *et al*. 2011b). The island was a centre of European trade so it was not surprising that many early collections were made here. Many species and subspecies have been described from type material first collected from the island such as the Rhinoceros Frog (*Limnonectes plicatellus*), Taylor's Frog (*Taylorana hascheana*), Western Malay River Terrapin (*Batagur affinis affinis*), Five-banded Gliding Lizard (*Draco quiquefasciatus*), Penang Banded Gecko (*Cyrtodactylus pulchellus*), Smith's Gecko (*Gekko smithii*), Olive Tree Skink (*Dasia olivacea*), Spotted Coral Snake (*Calliophis gracilis*) and the Striped Coral Snake (*C. intestinalis lineata*) (see Grismer 2011a; Gray 1835; Stoliczka 1870, 1873; Praschag *et al*. 2008). Amongst the earliest naturalist who reported on the herpetofauna from Penang were Theodore Edward Cantor in 1847 and Major Stanley Smyth Flower who collected there near the turn of the century (Cantor 1847; Flower 1896, 1899). Another prominent herpetologist was Ferdinand Stoliczka who collected at Penang Hill and described a numerous new species he discovered including the type species for the genus *Ansonia*, the Penang Slender Toad (*A. penangensis* (Stoliczka 1870)). Other species that originated from material collected at the higher elevations of the island include Penang Island Rock Gecko (*Cnemaspis affinis*), Indo-Malayan Mountain Pitviper (*Ovophis convictus*) and Red-bellied Reed Snake (*Calamaria albiventer*) (Inger & Marx 1965; Grismer *et al*. 2008; Malhotra *et al*. 2011).

On Langkawi island to the north, works in recent years have only started shedding light on the rich diversity of herpetofauna found there. Work on the island progressed in the late 1990's by Ibrahim Jaafar (Jaafar *et al*. 2006) and were later continued by Grismer and colleagues (Grismer *et al*. 2006c) and resulted in a number of new species being discovered there in the last decade such as the Monk's Rock

Gecko (*Cnemaspis monochorum*), Roti Canai Rock Gecko (*C. roticanai*), Tuberculate Bent-toed Gecko (*Cyrtodactylus macrotuberculatus*), Langkawi Island Forest Gecko (*Sphenomorphus langkawiensis*). The most recent additions to the herpetofauana of Langkawi Island are Mahsuri's Rock Gecko (*Cnemaspis mahsuriae*) and Gunung Raya Green-crested Lizard (*Bronchocela rayaensis*) from Gunung Raya (Grismer 2008; Grismer & Chan 2010; Grismer & Norhayati 2008; Grismer *et al*. 2009a, 2015a,c). Because of the location of the island archipelago that is sandwiched between Tenasserim-South Thailand semi-evergreen forest biome to the north and the evergreen Peninsular Malaysia rainforest to the south (Das & van Dijk 2013), the animals and plants here have a unique signature that reflects this meeting of the different zones. The Langkawi group of islands harbour a number of Indo-Chinese taxa not found further south in the country and some of these are not found on the mainland. Indochinese species such as Smith's Litter Frog (*Leptobrachium smithi*), Large-headed Frog (*Limnonectes macrognathus*), Nine-keeled Sun Skink (*Eutropis novemcarinata*), Black-spotted Litter Skink (*Scincella melanosticta*), *Cyrtodactylus brevipalmatus,* Bocourt's Water Snake (*Subsessor bocourti*), Green Cat Snake (*Boiga cyanea*), Beautiful Pit Viper (*Crypetlytrops venustus*) and the Small-spotted Coral Snake (*Calliophis maculiceps*) are known from here (Grismer *et al*. 2006c, 2015a; personal observation).

The islands are also significant because they have affiliations with Sundaland taxa which is reflected in their herpetofaunal composition by the presence of species such as *Macrocalamus lateralis* and *Calliophis intestinalis* (red-bellied form) that are both known from Gunung Raya, the highest peak on the island (personal observation). The genus *Macrocalamus* is a lineage unique to the Thai-Malay Peninsula and the centre of diversity for the genus are the mountains of Peninsular

Malaysia where they have radiated into seven currently recognised species (Lim 1963a; Vogel & David 1999; Norsham & Lim 2002; David & Pauwels 2004). The red-bellied *Calliophis intestinalis* is another species known from scattered localities in Borneo and Peninsular Malaysia where they are restricted to high elevations (Smedley 1931a; Stuebing *et al*. 2014).

2.2 Geographical history of Sundaland shaping upland habitats

Each of these mountain ranges supports their own unique assemblage of species and varying levels of local endemism. In the last decade dozens of new species have been added to the known list of upland herpetofauna (Chan *et al*. 2014a; David & Pauwels 2004; Grismer *et al*. 2012a, 2013a,b, 2014a,b, 2015a,b; Grismer & Quah 2015; Loredo *et al*. 2013; Matsui *et al*. 2009, 2014; Vogel & David 1999; Vogel *et al*. 2004; Wood *et al*. 2008, 2009; Zug 2010). The term "sky islands" has been used for these high-elevation habitats that are geographically subdivided and isolated among different mountain ranges (Heald 1951; McCormack *et al*. 2009). In oceanic archipelagos water acts as the barrier to dispersal. Similarly, in the case of sky islands, low-elevation habitat is the barrier to dispersal or different upland taxa, thus facilitating divergence and speciation in isolated populations (McCormack *et al*. 2009). This term encompasses a variety of upland habitats such as alpine meadows, cloud forest and plateaus, all of which are separated by tracts of lowland habitats such as savannah, grassland, desert or lowland forest that deter the spread of montane taxa. There are many sky island complexes scattered across the globe such as the Rocky Moutains, Madrean and Great Basin archipelagos in North America, the Pantepui region of Venezuela, Guyana and Northern Brazil, the Ethiopian Highlands, the volcanic mountains in the East African Arc and Cameroon, the Western Ghats in India and the Annamite Mountains in Indo-China (McCormack *et al*. 2009).

The geological history of these sky islands in turn act as generators for diversity over different spatial and temporal scales with natural selection and genetic drift driving speciation. In the case of Peninsular Malaysia, it was formed when terranes rifted from the eastern margin of Gondwana and collided with Eurasia in the Jurassic (Woodruff 2003a). The core of the country comprises of three tectono-stratigraphic zones, a western block, the Sibumasu Terrane of Early Permian origin and an eastern block, the Sukhothai Arc that sandwich a central belt, and both were assembled in the late Triassic (Metcalfe 2013). These various tectonic blocks that are now pieced together to form Peninsular Malaysia are of ancient origin and derived from the southern hemisphere supercontinent Gondwana (Metcalfe 1998). As such, the Thai-Malay Peninsula has existed for 100 Myr and throughout the Oligocene and Miocene the peninsula is thought to be similar in geographic extent and physiography as present day (Hall 2001, 2002, 2011, 2012; Woodruff 2003b; 2010). During the Pliocene and Pleistocene, the present day Malay Peninsula was part of a single large landmass called 'Sundaland' and was connected to islands of Borneo, Sumatra and Java as recently as 10,000 years ago (Wilting *et al*. 2012; Mollengraaff 1916). This was brought upon by the sequestering of ice during major glacial periods that resulted in global sea levels falling by as much as 120m. Ever-changing sea levels during glacial cycles led to the alternating exposure and submergence of land bridges connecting the mainland and island groups (Voris 2000; Sathiamurthy & Voris 2006). Thus, sea-level changes rather than large-scale tectonic changes have affected the basic geographic appearance of the peninsula (Woodruff & Turner 2009). More than 50 glacial-interglacial sea level fluctuations have occurred in the last 2.4 million years have had a far reaching effect on Sundaland flora and fauna (Heaney 1991; Roberts *et al*. 2011; Woodruff 2010; Woodruff & Turner 2009).

Voris (2000) noted that the period of time at or below particular sea levels and frequency at which the sea levels fell or rose were important factors in determining plant and animal dispersal. It was a sink or swim effect for the plants and animals in the late Pliocene and early Pleistocene as they had to negotiate a constantly changing matrix of available land bridges and suitable habitats in order to disperse through Sundaland (Bird *et al*. 2005).

Some authors have argued that an extensive savannah corridor existed during the last interglacial period when sea levels were lower and conditions drier despite temperatures being cooler. These vast tracts of open vegetation were predicted to have been barriers to the dispersal of rainforest-dependent species trapped in the upland refugia (Bird *et al*. 2005; Woodruff 2010; Woodruff & Turner 2009). However, a growing body data support the evidence for wider tracts of tropical and montane rainforest during the last glacial maxima. Model simulation have pointed to more extensive lowland and montane forest cover during each hypothermal phase (Cannon *et al*. 2009; Crucifix *et al*. 2005; Otto *et al*. 2002). Palynological studies have also supported the wider coverage of rainforest on the emergent Sunda Shelf during the interglacial period (Kershaw *et al*. 2001; Morley 2000). Meijaard, (2003) argued that the absence of mammals characteristic of open environments on the Natuna Islands as a strong indication that the region was forested and not covered in savannah as others had put forth during the last glacial maxima.

Temperatures in the past were also predicted to be much cooler than they were today as evidenced from the presence of glaciers on the islands of Borneo, Sumatra and New Guinea in the past and a snowline 1000 m lower than exists today (Heaney 1991; Morley & Flenley 1987). During past glacial periods when climates were expected to be cooler on the Sunda Shelf with estimated drops in temperature

between 3-6° (Cannon *et al*. 2009; Heaney 1991; Kershaw *et al*. 2007; Woodruff 2010; Wurster *et al*. 2010), displacement of sky island habitats to lower elevations meant that formerly isolated populations came into contact. Upland evergreen rainforest in Sundaland alone was estimated to have had a 30% greater range of coverage than they have currently (Cannon *et al*. 2009). The examination of pollen through palynology at various montane sites in Java, Sumatra and New Guinea indicate that montane vegetation zones were found at much lower elevation than at present day (Heaney 1991). The distribution of animals in turn is correlated with the distribution of plants and phenology (Woodruff 2010). Thus lowered montane vegetation zones would also indicate that montane animals would have had the opportunity to disperse to lower elevations as well. Subsequently, during interglacial periods when the climate warmed these populations would then have to retreat to their isolated mountain tops which could have driven allopatric speciation. Both lowland and montane rainforest would have responded to the refugial dynamics brought on by the glacial cycles in a similar way—maximum forest cover during glacial maxima and minimal forest cover during interglacials. The dual expansion of both forests was possible because the lowered sea levels exposed previously unavailable land areas for lowland forest to colonise while declining temperatures lowered the elevational zonation between upland and lowland forest (Cannon *et al*. 2009).

Depending on the length of the interglacial period, if enough time has passed, isolation at the different mountain peaks could have been conducive to divergence by genetic drift. Populations at the different locations would have also been subjected to different selection pressures (Avise 2000). With enough time, these separations could lead to allopatric speciation in the now separated mountain tops like what has been